



Assessing Africa-wide Pangolin exploitation by scaling local data

Ingram, Daniel J.; Coad, Lauren; Abernethy, Katharine A.; Maisels, Fiona; Stokes, Emma J.; Bobo, Kadir S.; Breuer, Thomas; Gandiwa, Edson; Ghiurghi, Andrea; Greengrass, Elizabeth; Holmern, Tomas; Kamgaing, Towa O. W.; Obiang, Anne-Marie Ndong; Poulsen, John R.; Schleicher, Judith; Nielsen, Martin Reinhardt; Solly, Hilary; Vath, Carrie L.; Waltert, Matthias; Whitham, Charlotte E. L.; Wilkie, David S.; Scharlemann, Jörn P. W.

Published in:
Conservation Letters

DOI:
[10.1111/conl.12389](https://doi.org/10.1111/conl.12389)

Publication date:
2018

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Ingram, D. J., Coad, L., Abernethy, K. A., Maisels, F., Stokes, E. J., Bobo, K. S., Breuer, T., Gandiwa, E., Ghiurghi, A., Greengrass, E., Holmern, T., Kamgaing, T. O. W., Obiang, A-M. N., Poulsen, J. R., Schleicher, J., Nielsen, M. R., Solly, H., Vath, C. L., Waltert, M., ... Scharlemann, J. P. W. (2018). Assessing Africa-wide Pangolin exploitation by scaling local data. *Conservation Letters*, 11(2), 1-9. [e12389].
<https://doi.org/10.1111/conl.12389>

LETTER

Assessing Africa-Wide Pangolin Exploitation by Scaling Local Data

Daniel J. Ingram¹, Lauren Coad^{1,2,3}, Katharine A. Abernethy^{4,5}, Fiona Maisels^{4,6}, Emma J. Stokes⁶, Kadiri S. Bobo⁷, Thomas Breuer⁶, Edson Gandiwa⁸, Andrea Ghiurghi⁹, Elizabeth Greengrass¹⁰, Tomas Holmern¹¹, Towa O. W. Kamgaing^{12,13}, Anne-Marie Ndong Obiang¹⁴, John R. Poulsen¹⁵, Judith Schleicher^{3,16}, Martin R. Nielsen¹⁷, Hilary Solly¹⁸, Carrie L. Vath^{19,20}, Matthias Waltert²¹, Charlotte E. L. Whitham²², David S. Wilkie⁶, & Jörn P.W. Scharlemann^{1,3}

¹ School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK

² Center for International Forestry Research, Jalan CIFOR Situ Gede, Sindang Barang Bogor (Barat) 16115, Indonesia

³ UN Environment World Conservation Monitoring Centre, 219 Huntingdon Road, Cambridge CB3 0DL, UK

⁴ African Forest Ecology Group, School of Natural Sciences, University of Stirling, UK

⁵ Institut de Recherches en Ecologie Tropicale, CENAREST, Gros Bouquet, Libreville, Gabon

⁶ Global Conservation Program, Wildlife Conservation Society, 2300 Southern Boulevard, NY 10460, USA

⁷ Department of Forestry, University of Dschang, P.O. Box: 222, Dschang, Cameroon

⁸ School of Wildlife, Ecology and Conservation, Chinhoyi University of Technology, Private Bag 7724, Chinhoyi, Zimbabwe

⁹ Independent Researcher, Rome, Italy

¹⁰ The Born Free Foundation, Holmwood, Broadlands Business Campus, Langhurstwood Road, Horsham RH12 4PN, UK

¹¹ Department of Biology, Norwegian University of Science and Technology, N-7491, Trondheim, Norway

¹² School for the Training of Wildlife Specialists Garoua, Ministry of Forestry and Wildlife, P.O. Box: 271 Garoua, Cameroon

¹³ Graduate School of Asian and African Area Studies, Kyoto University, Japan

¹⁴ Agence Nationale des Parcs Nationaux, Libreville, Gabon

¹⁵ Nicholas School of the Environment Duke University, Durham, NC, USA

¹⁶ Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK

¹⁷ Department of Food and Resource Economics, University of Copenhagen, Rolighedsvej 25, 1958 Frederiksberg C, Copenhagen, Denmark

¹⁸ Independent Researcher, Bolzano, Italy

¹⁹ Montana Tech, 1300 West Park Street, Butte, MT 59701, USA

²⁰ School of Natural Resources and Environment, University of Florida, Gainesville, FL, USA

²¹ Workgroup on Endangered Species, J.F. Blumenbach Institute of Zoology and Anthropology, Georg-August-Universität Göttingen, Göttingen, Germany

²² CzechGlobe - Global Change Research Institute, The Czech Academy of Sciences, Bělidla 986/4a, 60300 Brno, Czech Republic

Keywords

Africa; hunting; market; OFFTAKE; pangolins; trade; wild meat.

Correspondence

Daniel J. Ingram, School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK.
E-mail: D.Ingram@sussex.ac.uk, danieljohningram@gmail.com

Received

3 January 2017

Accepted

25 June 2017

Editor

Claire Kremen

doi: 10.1111/conl.12389

Abstract

Overexploitation is one of the main pressures driving wildlife closer to extinction, yet broad-scale data to evaluate species' declines are limited. Using African pangolins (Family: Pholidota) as a case study, we demonstrate that collating local-scale data can provide crucial information on regional trends in exploitation of threatened species to inform conservation actions and policy. We estimate that 0.4–2.7 million pangolins are hunted annually in Central African forests. The number of pangolins hunted has increased by ~150% and the proportion of pangolins of all vertebrates hunted increased from 0.04% to 1.83% over the past four decades. However, there were no trends in pangolins observed at markets, suggesting use of alternative supply chains. The price of giant (*Smutsia gigantea*) and arboreal (*Phataginus* sp.) pangolins in urban markets has increased 5.8 and 2.3 times respectively, mirroring trends in Asian pangolins. Efforts and resources are needed to increase law enforcement and population monitoring, and investigate linkages between subsistence hunting and illegal wildlife trade.

Introduction

Overexploitation is one of the main pressures causing species' declines and local extinctions (Maxwell *et al.* 2016; Ducatez & Shine 2017). Currently, broad-scale data on the exploitation of terrestrial wildlife, needed to inform conservation policy and action, are lacking (Joppa *et al.* 2016). Information on wildlife harvests can be difficult to collect because, at times, hunters and traffickers operate secretly to avoid law enforcement, and may be unwilling to disclose what they have harvested (Keane *et al.* 2008). Law enforcement and seizures data have been used to quantify exploitation of threatened species; however, these data suffer from detection biases and underestimation (Gavin *et al.* 2010). Instead, collating local-scale hunting studies may provide more accurate estimates of the number of animals hunted and relevant information to aid conservation efforts, complementing seizures data (Sánchez-Mercado *et al.* 2016).

Pangolins (Family: Manidae), a group of African and Asian scaly mammals, are considered to be "the most heavily trafficked wild mammal in the world," and are hunted and traded for food and traditional medicines (Challender *et al.* 2014). They are also used in rituals, art, and magic among communities across Africa (Soewu & Sodeinde 2015) and Asia (e.g., Mahmood *et al.* 2012). Despite a long history of exploitation, pangolin populations in Asia have declined dramatically (estimated 90% decline of Chinese pangolin [*Manis pentadactyla*] since the 1960s; Wu *et al.* 2004). All four Asian pangolin species are listed as "Critically Endangered" or "Endangered" on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species due to past, present, and predicted population declines driven by growing demand for meat and scales (Challender *et al.* 2014), and compounded by low reproductive rates (Newton *et al.* 2008; Challender *et al.* 2012; Cheng *et al.* 2017). In addition, commercial trade and international trade of wild-caught pangolins has been banned (CITES 2016).

In comparison to Asian pangolins, less is known about the African species: white-bellied (*Phataginus tricuspis*), black-bellied (*Phataginus tetradactyla*), giant ground (*Smutsia gigantea*), and Temminck's ground pangolin (*Smutsia temminckii*). They are currently classified as "Vulnerable" by the IUCN (Pietersen, Waterman *et al.* 2014; Waterman *et al.* 2014a,b; Waterman, Pietersen *et al.* 2014), and international trade was recently banned (CITES 2016). African pangolin populations are assumed to be declining, because of habitat degradation and loss (Challender *et al.* 2014), hunting, and increasing demand from international markets (Challender & Hywood 2012). However, little is known about population sizes, reproductive potential, and African pangolin trade.

Mounting evidence suggests that as the availability of Asian pangolins declines and international trade flows increase, traders are increasingly supplying the currently more abundant and less expensive African pangolins to meet Asian demand (Challender & Hywood 2012).

Seizures of pangolins and their derivatives (e.g., scales and skins) from Africa destined for Asia are increasing (Heinrich *et al.* 2016) with over 53 tons seized in 2013 (Flocken 2015), and more than 1 million pangolins trafficked globally since 2000 as estimated from illegal trade data (IUCN SSC Pangolin Specialist Group 2016). These estimates likely represent a fraction of all pangolins traded, and an even smaller proportion of the number of pangolins hunted.

Many studies have monitored wildlife hunting and/or markets at local scales across Africa (e.g., Crookes *et al.* 2006; Coad *et al.* 2013). Collating data from these studies allows us to infer trends, produce indicators of overall rarity and demand at a regional scale, and provide information to aid conservation efforts. Here, we collate data from local-scale hunting and market studies to provide the first comprehensive assessment of the exploitation of African pangolins by estimating: (1) the total number of pangolins hunted annually; (2) temporal trends in the proportion of pangolins of all animals hunted or observed at wild meat markets; and (3) trends in the price of pangolins over time as an indicator of changes in demand or rarity (Courchamp *et al.* 2006).

Materials and methods

Data

We collated data on the number of individual vertebrates hunted or observed at wild meat markets in a particular area and time period across Africa from a variety of "sources" (published papers, reports from nongovernmental organizations, PhD or Master's theses, or unpublished data collected using a published methodology) using a snowballing technique (Noy 2008), and searching reference lists and online libraries. Where sources did not provide detailed data on animals hunted or observed at markets, we contacted the authors for raw data. Where available, we extracted information on use (e.g., consumed, sold), hunting method (e.g., gun, snare), sex, age category (as assessed by the authors), and price of whole animals observed at markets.

Each source could contain one or more "studies," where each "study" collected data using a specific sampling methodology at a location, and was assigned a unique StudyID. Each study provided data on the location (hereafter "site"), market type (urban or rural), start and end date, species and number of individuals hunted

(hunting studies), hereafter referred to as “the catch,” or observed at wild meat markets (market studies), hereafter “markets.” Studies were included that collected data on all vertebrate taxa hunted/observed at market at a site within a specified time, i.e., we excluded single-taxon studies, e.g., those that only reported primate hunting, and partial sampling.

To investigate trends over time, we allocated data from studies to the years in which the data were collected. Studies spanning multiple years, including studies of less than a year's duration, were separated into annual “samples” if temporally resolved raw data were available and could be separated and allocated to a year ($n = 16$ studies). Studies that provided temporally unresolved data, i.e., one value per species for the entire study duration, were included if the study duration was ≤ 500 days to allow reasonable allocation of data to individual years, while including studies that sampled slightly longer than 1 year. All samples were allocated to a year by calculating the mid-date between the start and end dates.

Estimating total catch of pangolins in Central African forests

Most studies that have human population and hunting territory size data available were located in Central African forests; we therefore restricted the estimates of total pangolin catch to this region. We define Central African forests as the forests in Cameroon, Central African Republic, Equatorial Guinea, Gabon, Democratic Republic of Congo, and Republic of Congo. We used three methods to estimate the total annual catch of pangolins in Central African forests from hunting studies. For the first method, we calculated the median annual number of pangolins hunted per area multiplied by the total likely hunted forest area, calculated as the forest area within 10 km of a settlement (Text S1). For the other two methods, we calculated the median annual number of pangolins hunted per rural person multiplied by either of two independent estimates of the total rural population (CIESIN *et al.* 2011; UNPD 2014; see Text S1 and Figure S1). To assess change over time, we repeated the analyses for samples collected before and after 2000 (Text S2), to permit comparison with Heinrich *et al.* (2016) showing an increase in seizures of African pangolins destined for Asia after 2000.

Trends in pangolins hunted and observed at market

To investigate trends of pangolins hunted or observed at markets, we calculated the percentage of individuals

from all African pangolin species combined among the total number of vertebrates in the catch or at markets within each sample, from hunting or market studies, respectively. We fitted linear mixed effects models (Zuur *et al.* 2009) using the lme4 package (Bates *et al.* 2015) in R version 3.2.4 (R Core Team 2016), and selected the final model using backward model simplification based on likelihood ratio tests. Arcsine-transformed percentages of pangolins in the catch or at markets were modeled separately as the response variable (Andreano *et al.* 2015), with year and a second-order polynomial of year as fixed effects. As random factors we included StudyID nested within SourceID to control for some of the variation due to research methods and site, and Country to account for variation among countries. Within the statistical models, the percentages of pangolins were weighted by the total number of animals within each sample as a proxy for sample size. Furthermore, we assessed overall trends that may influence our results (such as body mass, accessibility, and sample duration, see Text S3, Text S4), and assessed whether the inclusion of the small number of early studies affected overall trends (Text S5).

Trends in prices

To investigate trends in prices of whole pangolin carcasses at markets, we adjusted all prices in Central African Francs (CFA) to 2015 prices by controlling for inflation using the consumer price index (CPI; The World Bank 2017). We fitted mixed effects models for arboreal and giant ground pangolins with log-transformed price as the response variable, interaction of year and market type (rural or urban) as a fixed effect, and SourceID as a random effect to control for some of the variation due to research methods and site. StudyID was not needed in these analyses because studies were not different from sources.

Separately, we calculated the price ratios of pangolins (averaged when multiple prices were reported per site and source) relative to three commonly hunted and similarly sized species using unadjusted prices, to control for changes in prices of traded vertebrates. We calculated price ratios for blue duiker (*Philantomba monticola*), African brush-tailed porcupine (*Atherurus africanus*), and greater cane rat (*Thryonomys swinderianus*), using fresh carcass prices where specified. We investigated price ratio trends for arboreal pangolins (*Phataginus* sp.) as insufficient price data were available for ground pangolins (*Smutsia* sp.). Mixed effects models were fitted for each of the prices ratios as described above.

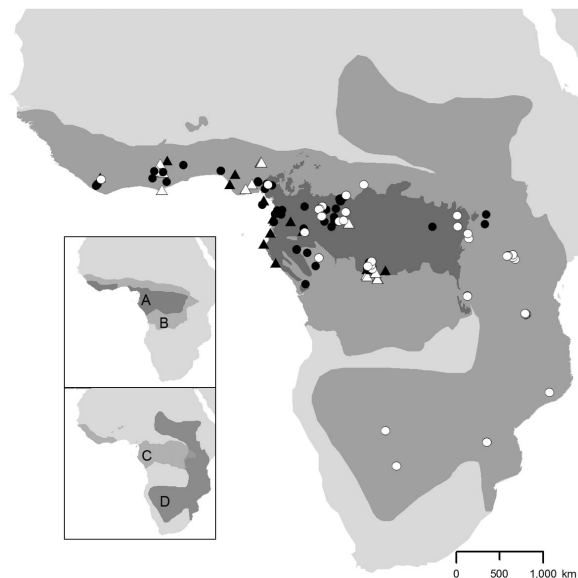


Figure 1 Sites where pangolins have been observed in the catch (filled circles) and at markets (filled triangles) from 113 hunting (circles) and 36 market (triangle) sites across Africa. Combined extent of occurrence (gray shading) for the four African pangolins (Pietersen, Waterman et al. 2014; Waterman et al. 2014a,b; Waterman, Pietersen et al. 2014), shown separately in insets for *P. tetradactyla* (A), *P. tricuspis* (B), *S. gigantea* (C), and *S. temminckii* (D). Central African forests shown as the WWF Tropical and Subtropical Moist Broadleaf Forests ecoregion clipped by Central African countries and the extent of occurrence of African pangolins (dark gray; Olson et al. 2001).

Results

Data

We collated data from 68 sources that met our inclusion criteria (Table S1), separated into 161 studies and 204 samples, accounting for 348,807 individual vertebrates. Of these, 152 samples had information on 71,716 individual vertebrates in the catch and 52 samples investigated 277,091 individuals at markets, of which 2,059 and 7,005 individuals were pangolins, respectively. Across all samples, 8,166 individuals were identified as arboreal pangolins (*Phataginus* sp.) and 300 as ground pangolins (*Smutsia* sp.), with a further 578 only identified to family (Manidae).

Pangolins were hunted at 71 of 113 (63%) sites in 10 of 14 (71%) countries, and observed at 18 of 36 (50%) markets in all seven countries for which we have data (Figure 1). On average, over time and across countries, per sample, pangolins represented $2.1 \pm 0.27\%$ (mean \pm SE) of vertebrates in the catch and $1.4 \pm 0.23\%$ at markets.

The sex composition of pangolins in the catch was 49% female, 45% male, with 6% of unknown sex ($n =$

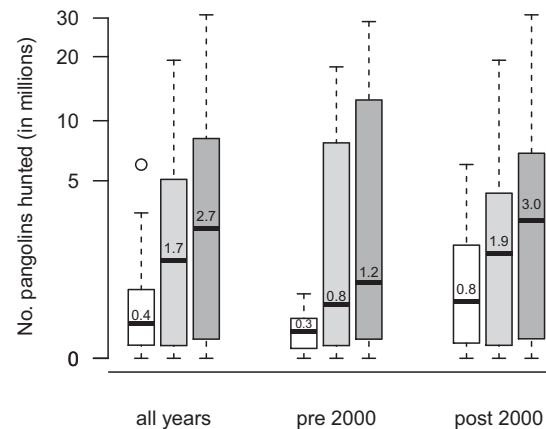


Figure 2 Estimates of the annual number of pangolins (*Phataginus* sp. and *S. gigantea* combined) hunted in Central African forests, median (thick lines) across all years (1975–2014; $n = 24, 44, 44$ samples), pre-2000 ($n = 8, 12, 12$), and post-2000 ($n = 16, 32, 32$), based on a forest area-based method (white), and UNPD-derived (light gray) and GRUMP-derived (dark gray) human population-based methods. Box plots show median, 1st and 3rd quartiles, with whiskers extending to extreme values no more than 1.5 times the length of the box, and points represent outliers.

560 pangolins from 10 sources). Most (50%) were adults, 45% juveniles and subadults, and 5% of unknown age ($n = 310$ pangolins, 5 sources). Pangolins were hunted by traps and snares (54%), hand (25%), gun (16%), or other means (5%) ($n = 822$ pangolins, 14 sources). Pangolins were either directly consumed (50%), sold (41%), or given as gifts (9%) ($n = 425$ pangolins, 9 sources).

Estimating total catch of pangolins in Central African forests

We estimate that between 0.42 and 2.71 million pangolins (*Phataginus* spp. and *S. gigantea*) were hunted each year in Central Africa (sampled range 1975–2014), with the two human population-based methods giving higher estimates of 1.68 million (0.22–4.76 interquartile range) and 2.71 million (0.35–7.66) pangolins (Figure 2; Table S1 and Figure S2). The total annual catch of pangolins has increased by an estimated 145–151% from before 2000 (range 1975–1999) to post-2000 (2000–2014) depending on estimation method (Figure 2). *S. temminckii* does not occur in Central African forests, and insufficient data were available to estimate total annual catch where it occurs.

Trends in pangolins hunted and observed at markets

The percentage of pangolins in the catch increased significantly from 0.04% in 1972 to 1.83% in 2014 (Figure 3A, minimum adequate model: percentage of

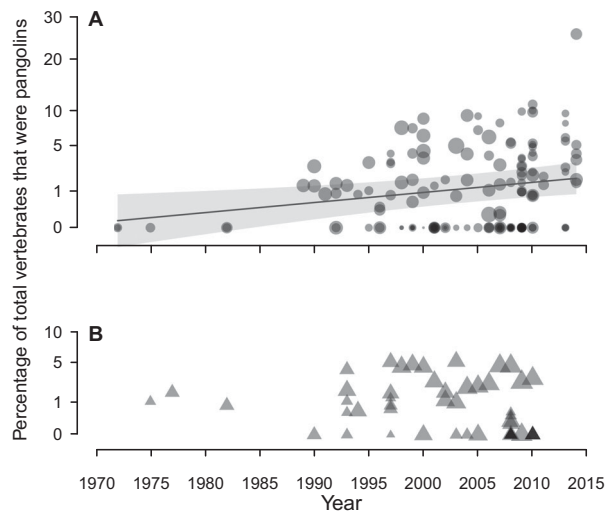


Figure 3 Trends in the percentage of vertebrates that were pangolins (Manidae) in the catch (A, $n = 152$ samples) and that were observed at markets (B, $n = 52$) across Africa. Samples shown as translucent points to show density of samples and are scaled by total catch of individual vertebrates (1–30,196 individuals). Trend line and 95% CI (shading) fitted using a linear mixed effects model.

pangolins = year + random effects of StudyID nested within SourceID, and Country, $\chi^2_{5,6} = 6.4$, $P = 0.012$). For comparison, we also found no temporal trends for the main hunted taxonomic groups (Cetartiodactyla and Rodentia; Figure S3), but we did find that pangolins account for more of the catch in the most accessible areas (Figure S4). The percentage of pangolins observed at markets did not change significantly between 1975 and 2010 (Figure 3B; $\chi^2_{4,5} = 1.9$, $P = 0.17$).

Trends in price

We collated price data for arboreal ($n = 149$ records) and giant ground ($n = 32$) pangolins from 31 sources in five countries. Prices for arboreal pangolins changed significantly over time, and changes differed depending on market type (Figure 4A, interaction: $\chi^2_{6,8} = 8.0$, $P = 0.02$; urban markets increasing from ~3,700 to 8,500 Central African Francs [CFA] and rural markets decreasing slightly from 3,200 to 2,700 CFA). The price of giant ground pangolins increased significantly at urban markets between 1993 and 2014 from approximately 24,000 to 140,000 CFA (Figure 4B; $\chi^2_{3,4} = 3.9$, $P = 0.05$), but not in rural ones where we have few prices ($n = 8$).

We calculated price ratios for blue duikers ($n = 134$ price records), brush-tailed porcupines ($n = 134$), and cane rats ($n = 82$) based on data from 31 sources collected at 85 sites in five countries between 1992 and 2014 (Table S1). Price ratios of arboreal pangolins to blue duik-

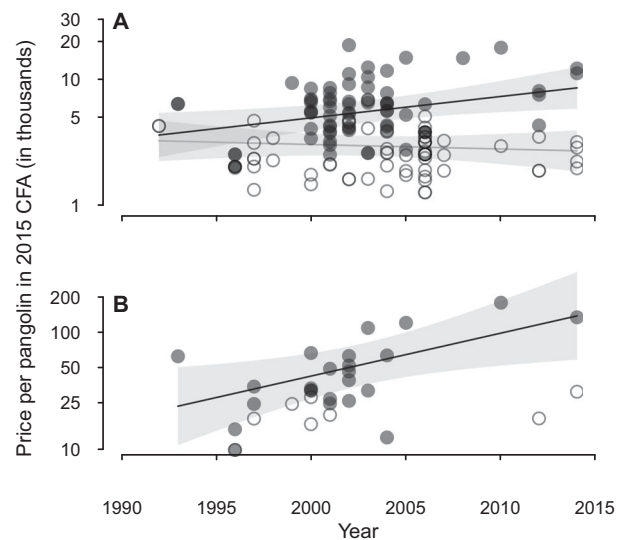


Figure 4 Trends in the price (in 2015 CFA) of arboreal pangolins (A, $n = 149$, *Phataginus* sp.) and of giant ground pangolins (B, $n = 32$, *S. gigantea*) at urban (filled points) and rural (hollow points) markets in Central Africa, plotted on a log scale. Statistically significant ($P < 0.05$) trend lines (black for urban, gray for rural) and 95% CI (shading) are fitted using linear mixed effects models.

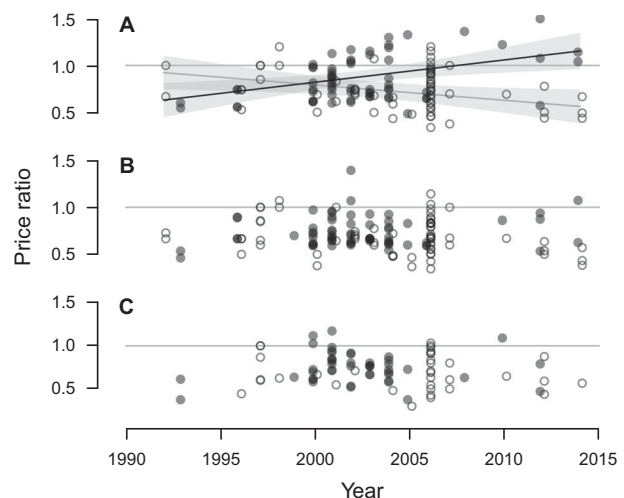


Figure 5 Trends in the price ratio at urban (filled points) and rural (hollow points) markets across Central Africa for arboreal pangolins (*Phataginus* sp.) to blue duikers (A, $n = 134$ price ratios), brush-tailed porcupines (B, $n = 134$), and greater cane rats (C, $n = 82$). Trend lines and 95% CI (shading) are fitted using linear mixed effects models, statistically significant ($P < 0.05$) in A for both urban (black line) and rural (gray line) markets.

ers increased significantly in urban markets (0.024 ± 0.008 ratio increase per year \pm SE, Figure 5A, Figure S5), and decreased in rural markets (-0.017 ± 0.007 ratio decrease per year; interaction of year and market type, $\chi^2_{5,6} = 12.9$, $P = 0.0003$). We found no significant interaction

of year and market type for the price ratio with porcupines ($\chi^2_{5,6} = 3.0$, $P = 0.08$) or cane rats ($\chi^2_{5,6} = 0.06$, $P = 0.81$), or any effect of year on the price ratios for porcupines ($\chi^2_{3,4} = 0.03$, $P = 0.87$) or cane rats ($\chi^2_{3,4} = 0.01$, $P = 0.93$).

Discussion

By collating local-scale studies, we provide the first regional estimates of African pangolin exploitation, revealing that pangolins are hunted and observed at markets throughout West and Central Africa, and that pressure from hunting has increased. The proportion of pangolins in the catch increased significantly over time, while the proportion observed at markets remained unchanged. We found evidence that the price of whole pangolins increased significantly at urban markets, but not at rural ones.

We estimate that 0.4–2.7 million pangolins (*P. tricuspis*, *P. tetradactyla*, and *S. gigantea*) were hunted annually in Central African forests, based on forest area- or human population-based extrapolations of average hunting levels. Our area-based estimate of ~420,000 pangolins hunted annually is consistent with a previous area-based estimate of ~400,000 *P. tricuspis*, and ~100,000 *S. gigantea* annually in Central Africa, although based on fewer studies and excluding *P. tetradactyla* (Fa & Peres 2001). Studies rely on the willingness of hunters to participate, so studies may represent only a subset of hunters at a particular site. Furthermore, hunters and traders may either fail to report illegally hunted protected species, or may not participate in studies; therefore, our extrapolations are likely conservative.

Our analyses suggest that the number of pangolins hunted has increased. Comparing forest area- or population-based extrapolations of data from before and after 2000, we found an ~150% increase, although interquartile ranges overlap likely due to relatively small sample sizes. When analyzing hunting samples, the percentage of pangolins out of the total catch increased significantly from ~0% to ~2% over four decades. The percentage of pangolins observed at markets remained unchanged, suggesting pangolins may be traded along alternative supply chains as observed in Ghana where pangolins were often traded to wholesalers away from wild meat markets (Boakyee *et al.* 2016), and in Gabon where Asian industry workers buy pangolins directly from hunters (Mambeya *et al.* unpublished). The reliability of market studies to assess exploitation has been questioned (Crookes *et al.* 2006) because individuals observed at markets likely represent a fraction of those hunted as traders hide illegal goods to avoid law enforcement. We

cannot discern whether the observed increase in pangolins hunted is caused by: (1) increased consumption, (2) increased hunting of smaller mammals due to declines in larger species (Ingram *et al.* 2015), (3) changes in hunting technology, and/or (4) increased demand from international markets (Challender & Hywood 2012).

We provide evidence that current hunting of African pangolins is likely unsustainable. On average, 45% of individuals were either juveniles or subadults, an indicator of overexploitation (Weinbaum *et al.* 2013), although aging subadults is difficult and our assessment relies on the authors reporting of age. This is of concern because pangolins take up to 2 years to reach sexual maturity and produce only one pup annually (Soewu & Sodeinde 2015), suggesting many of the pangolins hunted had not reproduced. Traps and snares were the most common hunting method (54%), however, the use of wire snares is illegal in all pangolin range states because they are effectively “blind” to the species trapped, but law enforcers often ignore or tolerate snaring (LAGA 2015). Effective law enforcement is needed, and should include stricter controls of snaring, such as snare specialist teams (Gandiwa *et al.* 2013), the elimination of corruption, and the provision of alternative protein sources and incomes.

We found substantial price increases for giant ground pangolins at urban markets, which may suggest that early signs of increased demand may not yet have been passed down to rural hunters, or that prices are responding to increased demand that is unmet by hunters because of depletion. We found small increases in prices and price ratios for arboreal pangolins in urban markets that, while increasing slowly, appear to be following the increasing trend of prices in Asia (Newton *et al.* 2008). Anecdotal evidence suggests that rural hunters may not yet know the value of pangolins elsewhere (Mambeya *et al.* unpublished).

While CITES provides a mandate for sustainable international wildlife trade, recently banning trade of all pangolin species (CITES 2016), it does not provide enforcement mechanisms on the ground. To implement the trade ban, governments, law enforcement officials, and conservationists need to better understand the supply chains of pangolins from Africa and Asia, to implement an appropriate monitoring program, and to increase the capacity to enforce the ban and intercept illegal shipments. To better target and inform conservation efforts, tailored survey methods to accurately estimate pangolin abundance and collect vital ecological data are needed. In addition, efforts should focus on determining local demand, and when/where this leads to unsustainable hunting. For cases where pangolin hunting is unsustainable, efforts should be made to improve and increase domestic law enforcement, increase public

awareness, reduce indiscriminate hunting methods such as snaring, and work with local communities to find effective solutions. Next steps should involve investigating harvests and enforcing legislations in support of country-wide conservation efforts. In addition, it is imperative that China, as one of the main consumers, considers implementation of awareness campaigns as well as increased monitoring, law enforcement, and penalties. Pangolins have attracted conservation attention recently, and as people become increasingly aware of the focus on pangolin hunting, the perceptions and stigmas of pangolin hunting are also likely to change over time.

Using African pangolins as a case study, we have demonstrated that collating local-scale data from hunting and market studies can be used to assess regional trends in wildlife exploitation. Local-scale data complement seizures data, by providing estimates of local demand and more accurate estimates of total hunting rates. Together, these types of data give insights into different aspects of pangolin use and trade, and paint a more complete picture of pangolin exploitation. In the absence of continent-wide species monitoring programs, collating local-scale data can highlight pressures on wildlife, and provide detailed quantitative information on wildlife exploitation that are crucial to inform conservation action and policy.

Acknowledgments

We thank all researchers and organizations that contributed data to the OFFTAKE database (www.offtake.org) and Luca Börger for statistical advice. We acknowledge support from the School of Life Sciences, University of Sussex for a doctoral training grant for DJI. Support for individual studies can be found in Acknowledgments S1.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Human population density (Balk *et al.* 2006; CIESIN *et al.* 2011) in Central Africa (Cameroon, Central African Republic, Equatorial Guinea, Gabon, Democratic Republic of Congo, Republic of Congo) classified into groups by standard deviation, and clipped by forest distribution (Schepaschenko *et al.* 2015) and pangolin extent of occurrence (IUCN 2014).

Figure S2. Studies with information on hunters and rural human population (white triangles) and hunter territory size (black circles) mapped on top of forest area (gray shading; Schepaschenko *et al.* 2015) in Central Africa.

Figure S3. Trends in the percentage of vertebrates that were Cetartiodactyla (A) and Rodentia (B) in the catch over time across Africa. Samples shown as translucent points to show density of samples and are scaled by total catch of individual vertebrates.

Figure S4. The percentage of vertebrates that were pangolins in the catch related to accessibility.

Figure S5. Trends in prices of blue duikers (A,D), brush-tailed porcupines (B,E), and cane rats (C,F) from studies that also contained data on arboreal pangolins (A-C) or giant ground pangolins (D-F) at urban (black points) and rural (gray points) markets. Prices are in 1,000 CFA adjusted to 2015 prices using the CPI (The World Bank 2017).

Table S1. Sources used in analyses and the countries in which data were collected. Crosses (X) indicate the analyses in which a data source was included.

References

- Andreano, A., Rebora, P. & Valsecchi, M.G. (2015). Measures of single arm outcome in meta-analyses of rare events in the presence of competing risks. *Biometrical J.*, **57**, 649–660.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, **67**, 51.
- Boakye, M.K., Kotzé, A., Dalton, D.L. & Jansen, R. (2016). Unravelling the pangolin bushmeat commodity chain and the extent of trade in Ghana. *Hum. Ecol.*, **44**, 257–264.
- Center for International Earth Science Information Network (CIESIN), Columbia University, International Food Policy Research Institute (IFPRI), The World Bank, and Centro Internacional de Agricultura Tropical (CIAT) (CIESIN *et al.*) (2011). *Global rural-urban mapping project, version 1 (GRUMPv1): population count grid*. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY. <https://doi.org/10.7927/H4VT1Q1H>. Accessed 3 May 2016.
- Challender, D.W.S. & Hywood, L. (2012). African pangolins under increased pressure from poaching and intercontinental trade. *Traffic Bull.*, **24**, 53–55.
- Challender, D.W.S., Baillie, J.E.M., Waterman, C. & IUCN-SSC Pangolin Specialist Group. (2012). Catalysing conservation action and raising the profile of pangolins – the IUCN-SSC Pangolin Specialist Group (PangolinSG). *Asian J. Conserv. Biol.*, **1**, 140–141.
- Challender, D.W.S., Waterman, C. & Baillie, J.E.M. (2014). Scaling up pangolin conservation. IUCN SSC pangolin specialist group conservation action plan. *Zoological Society of London*. London, UK.
- Cheng, W., Zing, S. & Bonebrake, T. C. (2017). Recent pangolin seizures in China reveal priority areas for intervention. *Conserv. Lett.* <https://doi.org/10.1111/conl.12339>.

- Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). (2016). Amendments to appendices I and II of the convention adopted by the Conference of the Parties at its 17th meeting, Johannesburg (South Africa), 24 September. 4 October 2016. Document No. 2016/063. Geneva, Switzerland. Available at <https://cites.org/eng/cop/index.php>. Accessed 1 January 2017.
- Coad, L., Schleicher, J., Milner-Gulland, E.J., *et al.* (2013). Social and ecological change over a decade in a village hunting system, central Gabon. *Conserv. Biol.*, **27**, 270–280.
- Courchamp, F., Angulo, E., Rivalan, P., *et al.* (2006). Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biol.*, **4**, e415.
- Crookes, D.J., Ankudey, N. & Milner-Gulland, E.J. (2006). The value of a long-term bushmeat market dataset as an indicator of system dynamics. *Environ. Conserv.*, **32**, 333–339.
- Ducatez, S. & Shine, R. (2017). Drivers of extinction risk in terrestrial vertebrates. *Conserv. Lett.*, **10**, 186–194.
- Fa, J.E. & Peres, C.A. (2001). Game vertebrate extraction in African and Neotropical forests: an intercontinental comparison. Paags 203–241 in J.D. Reynolds, G.M. Mace, J.G. Robinson, K.H. Redford, editors. *Conservation of exploited species*. Cambridge University Press, Cambridge.
- Flocken, F. (2015). Listing pangolins under US Endangered Species Act. <http://www.ifaw.org/united-kingdom/news/listing-pangolins-under-us-endangered-species-act>. Accessed 18 December 2016.
- Gandiwa, E., Heitkönig, I.M.A., Lokhorst, A.M., Prins, H.H.T. & Leeuwis, C. (2013). Illegal hunting and law enforcement during a period of economic decline in Zimbabwe: a case study of northern Gonarezhou National Park and adjacent areas. *J. Nat. Conserv.*, **21**, 133–142.
- Gavin, M.C., Solomon, J.N. & Blank, S.G. (2010). Measuring and monitoring illegal use of natural resources. *Conserv. Biol.*, **24**, 89–100.
- Heinrich, S., Wittman, T.A., Prowse, T.A.A., *et al.* (2016). Where did all the pangolins go? International CITES trade in pangolin species. *Glob. Ecol. Conserv.*, **8**, 241–253.
- Ingram, D.J., Coad, L., Collen, B., *et al.* (2015). Indicators for wild animal offtake: methods and case study for African mammals and birds. *Ecol. Soc.*, **20**, 40.
- International Union for Conservation of Nature (IUCN). (2014). *Phataginus tetradactyla*. The IUCN Red List of Threatened Species. Version 2016-3. <https://www.iucnredlist.org>. Accessed 4 September 2016.
- IUCN SSC Pangolin Specialist Group. (2016). The conservation status, illegal trade and use of pangolins (*Manis spp.*). Information document for the 66th meeting of the CITES standing committee, 11–15 January 2016, Geneva, Switzerland, pp 1–8. Accessed 3 February 2017.
- Joppa, L.N., O'Connor, B., Visconti, P., *et al.* (2016). Filling in biodiversity threat gaps. *Science*, **352**, 416–418.
- Keane, A., Jones, J.P.G., Edwards-Jones, G. & Milner-Gulland, E.J. (2008). The sleeping policeman: understanding issues of enforcement and compliance in conservation. *Anim. Conserv.*, **11**, 75–82.
- Last Great Ape Organization (LAGA) (2015). Annual Report January–December 2015. Cameroon. http://www.laga-enforcement.org/Portals/0/Activity%20reports%202015/LAGA_Annual_Report%202015.pdf. Accessed 18 December 2016.
- Mahmood, T., Hussain, R., Irshad, N., Akrim, F. & Nadeem, M.S. (2012). Illegal mass killing of Indian pangolin (*Manis crassicaudata*) in Potohar region, Pakistan. *Pak. J. Zool.*, **44**, 1457–1461.
- Maxwell, S.L., Fuller, R.A., Brooks, T.M. & Watson, J.E.M. (2016). The ravages of guns, nets and bulldozers. *Nature*, **536**, 143–145.
- Newton, P., Nguyen, V.T., Robertson, S. & Bell, D. (2008). Pangolins in peril: using local hunters knowledge to conserve elusive species in Vietnam. *Endanger. Species Res.*, **6**, 41–53.
- Noy, C. (2008). Sampling knowledge: the hermeneutics of snowball sampling in qualitative research. *Int. J. Soc. Res. Methodol.*, **11**, 327–344.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., *et al.* (2001). Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience*, **51**, 933–938.
- Pietersen, D., Waterman, C., Hywood, L., Rankin, P. & Soewu, D. (2014). *Smutsia temminckii*. The IUCN Red List of Threatened Species 2014: e.T12765A45222717. <https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12765A45222717.en>. Accessed 13 December 2016.
- R Core Team (2016). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Sánchez-Mercado, A., Asmussen, M., Rodríguez-Clark, K.M., Rodríguez, J.P. & Jedrzejewski, W. (2016). Using spatial patterns in illegal wildlife uses to reveal connections between subsistence hunting and trade. *Conserv. Biol.*, **30**, 1222–1232.
- Schepaschenko, D., See, L., Lesiv, M., *et al.* (2015). Development of a global hybrid forest mask through the synergy of remote sensing, crowdsourcing and FAO statistics. *Remote Sens. Environ.*, **162**, 208–220.
- Soewu, D.A. & Sodeinde, O.A. (2015). Utilization of pangolins in Africa: fuelling factors, diversity of uses and sustainability. *Int. J. Biodivers. Conserv.*, **7**, 1–10.
- The World Bank. (2017). Consumer price index (2010 = 100). International Monetary Fund, International financial statistics and data files. <http://data.worldbank.org/indicator/FP.CPI.TOTL>. Accessed 15 April 2017.
- UNPD. (2014). *World urbanization prospects, the 2014 revision*. United Nations, Department of Economic and Social Affairs, Population Division (UNPD). Accessed 28 November 2016.

- Waterman, C., Pietersen, D., Soewu, D., Hywood, L. & Rankin, P. (2014a). *Phataginus tetradactyla*. The IUCN Red List of Threatened Species 2014: e.T12766A45222929. <https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12766A45222929.en>. Accessed 13 December 2016.
- Waterman, C., Pietersen, D., Soewu, D., Hywood, L. & Rankin, P. (2014b). *Phataginus tricuspis*. The IUCN Red List of Threatened Species 2014: e.T12767A45223135. <https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12767A45223135.en>. Accessed 13 December 2016.
- Waterman, C., Pietersen, D., Hywood, L., Rankin, P. & Soewu, D. (2014). *Smutsia gigantea*. The IUCN Red List of Threatened Species 2014: e.T12762A45222061. <https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12762A45222061.en> (Visited Dec. 2016). Accessed 13 December 2016.
- Weinbaum, K.Z., Brashares, J.S., Golden, C.D. & Getz, W.M. (2013). Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecol. Lett.*, **16**, 99–111.
- Wu, S., Liu, N., Zhang, Y. & Ma, G. (2004). Assessment of threatened status of Chinese pangolin (*Manis pentadactyla*). *Chinese J. Appl. Environ. Biol.*, **10**, 456–461.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. Springer-Verlag, Berlin.